Observations on the Understory Climbing Fern, *Polybotrya pubens* (Dryopteridaceae) in a Peruvian Rain Forest

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The neotropical fern genus *Polybotrya* has 35 species, all of which grow in old-growth wet forests and most of which (33) grow along the leaf litter of the forest floor until reaching an object they can climb to 1–10 m in height (Moran, 1987a). This growth habit is also found in *Lomagramma* and *Lomariopsis*, and certain species of *Arthropteris, Bolbitis, Lemmaphyllum, Maxonia, Microgramma, Microsorium*, and *Olfersia* (Page, 1979; Tryon and Tryon, 1982; Moran, 1986), in addition to many other plant groups.

The production of fertile leaves by most species of *Polybotrya* is virtually dependent on climbing, as nonclimbing individuals only rarely develop spore-bearing leaves (Moran, 1987b). In this study, we report observations and measurements of *Polybotrya pubens* C. Martius in an initial attempt to determine the factors affecting this fern species' climbing of trees, and, by inference, its potential to produce fertile leaves.

STUDY AREA AND METHODS

The study area was located at 350 m in the Palcazu valley of central Peru (province of Oxapampa, department of Pasco, 10°10′S and 75°15′W), 1.5 km from the Amuesha settlement of Quebrada Castillo and about 8 km west of the town of Iscozacin, along the Omaiz river. A rain gauge located in Iscozacin received 604 cm of precipitation in 1984 (Aguilar Delgado, 1986), and this appears to be a typical amount for the area. Topographical relief in the study area was minor, with an elevational range of only 30 m. However, there were changes in soil types present, with reddish-brown clays on slopes and in ravines, and light gray-brown sandy loams on small, flat upland areas. In a previous study, we found *Polybotrya pubens* to be seven times more abundant in the uplands (Young & León, 1989). We chose one upland site for this study that had no obvious human-caused disturbance. The site had a tall (25 m) tree canopy, a uniformly dense understory, and trees and shrubs of all size classes.

In June 1987, we studied every climbing and nonclimbing *Polybotrya pubens* found within five 2-m wide transects of variable length (11–46 m) that were placed 10 m apart. A total surface area of 354 m^2 was surveyed. Treefall gaps were excluded as *P. pubens* does not grow in them. Each *P. pubens* individual was carefully excavated or removed from its climbing support and disentangled. Rhizome length was measured and the number of living leaves and persistent petiole bases (i.e., total number of leaves present or formerly present) counted. Because the oldest section of the rhizome decomposes, all measurements of rhizome length were necessarily minimal estimates of total rhizome growth. No rhizomes were observed to have forked.

For climbing individuals, we also measured the diameter of the tree climbed, and, if the plant was rooted in the soil, the distance from the base of the support to the apex of the rhizome. For nonclimbing individuals, we measured the distance between the growing point of the rhizome and the nearest possible vertical support element 1 cm in diameter.

Results

One hundred seventy-eight individuals of *Polybotrya pubens* were present, giving a density of 0.5 plants/m^2. Of these, 85% (151) were terrestrial, located in the litter layer or on rotted logs and had 25 ± 2 cm (mean $\pm$ SE) long rhizomes. The remainder were climbing live or dead trees and had 46 ± 12 cm rhizomes. Climbers had significantly longer rhizomes than nonclimbers ($p < 0.04$; Wilcoxon two-sample test).

Most of the population sampled, both climbing and terrestrial, had rhizomes <30 cm long. The right skew of the distribution of rhizome-length size classes of nonclimbing individuals (Fig. 1) suggests that there was either considerable mortality or little growth within the smaller size classes, because relatively few individuals were longer than 40 cm. The comparative lack of skew in the distribution of rhizome-length size classes of climbing individuals (Fig. 1) suggests that climbers grow quickly and thus pass into larger size classes. Only one individual had fertile leaves, a climber that also had by far the longest rhizome (251 cm).

Rhizomes of climbing *Polybotrya pubens* were mostly adpressed against their supports and usually extended upward, although sometimes they had doubled back or even descended. The direction of rhizome growth of nonclimbers was also quite unpredictable: sometimes the rhizomes had twisted >360°. The rhizomes had probably changed direction as they encountered obstacles, such as branches, which had since disappeared. Also, the rhizomes rolled to some extent on their longitudinal axes during growth as the emergence of each alternate frond would slightly change the orientation of the rhizome tips. In terrestrial individuals, these tips lay on the surface of the leaf litter, while the oldest sections of the rhizomes could be found buried under up to 3 cm of litter.

Number of petiole bases was highly correlated with the length of the rhizome ($r = 0.86$; d.f. = 176; $p < 0.001$), suggesting that new leaves are produced regularly as the rhizome grows. However, no matter what the length of the rhizome, the number of living leaves was relatively constant and as a result weakly correlated with rhizome length ($r = 0.24$; d.f. = 161; $p < 0.001$). There appeared to be no differences between climbers and nonclimbers in these relationships.

Twenty of the climbers were rooted solely on their supports, having either germinated there as epiphytes or, more probably, having lost contact with the

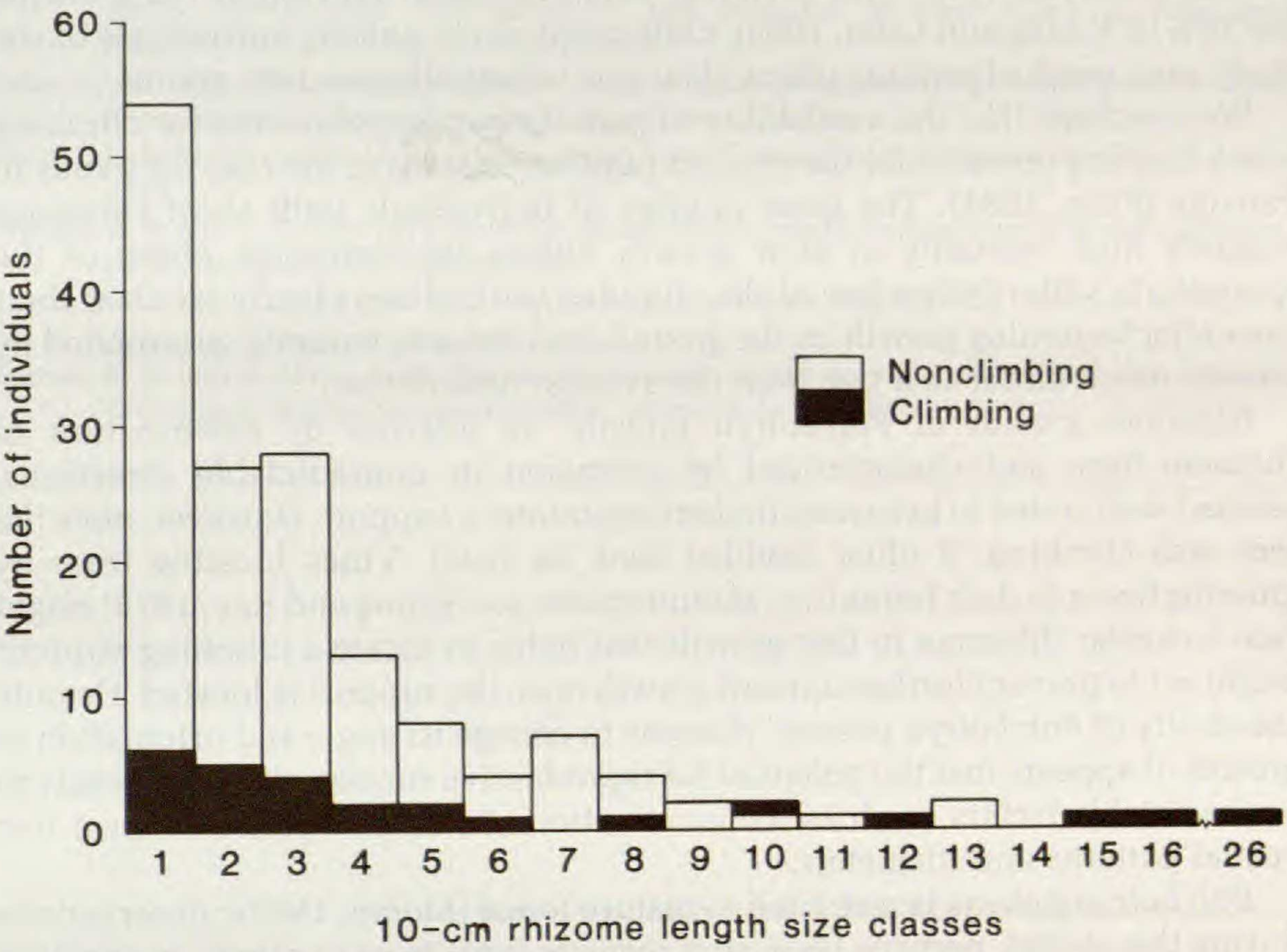

FIG. 1. Distributions of size classes of climbing and nonclimbing individuals of *Polybotrya pubens*. Size classes given are 10-cm increments of rhizome length.

ground (secondary hemi-epiphytes). Only seven climbers were also rooted in the soil. The trees climbed by these 27 plants were relatively large, with a mean basal diameter of 6 ± 1 cm.

The average rhizome length of nonclimbing *Polybotrya pubens* was significantly less than the distance (56 ± 3 cm) the plants would have had to grow in order to reach the nearest tree 1≥cm in diameter ($p<0.001$; Wilcoxon two-sample test). Thus, the distance to and availability of vertical supports were potential limiting factors for this population. The seven climbers rooted in the soil had first travelled a minimum of 19 ± 6 cm in order to reach the trees that they climbed; this was almost three times less than the average distance of nonclimbers to suitable tree stems.

DISCUSSION

The abundance of *Polybotrya pubens* measured in this study was the same as that found on a 10 by 20 m plot located about 0.5 km away (0.5 plants/m^2; Young and León, 1989). The percentage of climbing individuals found during the present study, however, was even less than that found previously (15% versus the 25% of Young and León, 1989). Only rarely do *P. pubens* individuals in the study area reach situations where they can potentially produce spores.

We conclude that the availability of suitable support elements for climbing was a limiting resource for the studied population, as was the case for lianas in Panama (Putz, 1984). The great number of individuals with short rhizomes suggests high mortality or slow growth during the terrestrial phase of the sporophyte's life. Only a few of the climbing individuals clearly reached their trees after beginning growth on the ground, and these apparently germinated by chance much closer to a tree than the average nonclimber.

Rhizome growth of *Polybotrya pubens*, as inferred by examination of rhizome form and characterized by extension in unpredictable directions, seemed well suited to help nonclimbers encounter a support. However, once the fern was climbing, it often doubled back on itself. Vines locating trees by growing towards dark forms (i.e., skototropism; see Strong and Ray, 1975) might face a similar dilemma in that growth that helps to locate a climbing support might act to prevent further upward growth once the support is located. Despite the ability of *Polybotrya pubens'* rhizome to change its angle and orientation of growth, it appears that the potential for reproductive success was due mostly to unpredictable factors, such as the germination site of the spore and local tree spatial patterns and diameters.

Polybotrya pubens is restricted to mature forest (Moran, 1987a; observations during this study), perhaps because it requires large trees to climb, in addition to requiring the relatively stable microenvironment of the tropical rainforest understory. Treefalls and regrowth vegetation have much more extreme environmental conditions (e.g., Chazdon & Fetcher, 1984) and offer an array of smaller-diameter support elements to climbing plants.

To expand upon these observations, data are needed on the rates of growth of climbing and nonclimbing *P. pubens*, and the length of time nonclimbers can persist on the forest floor without reaching suitable trees to climb.

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